



# Editorial: Recent Insights Into the Double Role of Hydrogen Peroxide in Plants

Naser A. Anjum<sup>1\*†</sup>, Sarvajeet Singh Gill<sup>2\*†</sup>, Francisco J. Corpas<sup>3</sup>,  
Cristina Ortega-Villasante<sup>4</sup>, Luis E. Hernandez<sup>5</sup>, Narendra Tuteja<sup>6</sup>, Adriano Sofo<sup>7</sup>,  
Mirza Hasanuzzaman<sup>8</sup> and Masayuki Fujita<sup>9</sup>

<sup>1</sup> Department of Botany, Aligarh Muslim University, Aligarh, India, <sup>2</sup> Stress Physiology and Molecular Biology Lab, Centre for Biotechnology, MD University, Rohtak, India, <sup>3</sup> Department of Biochemistry, Cell and Molecular Biology of Plants, Experimental Station of Zaidin, Spanish National Research Council (CSIC), Granada, Spain, <sup>4</sup> Fisiología Vegetal (Plant Physiology Laboratory), Dpto. Biología (Biology Department), Universidad Autónoma de Madrid, Madrid, Spain, <sup>5</sup> Laboratory of Plant Physiology, Department of Biology/Research Centre for Biodiversity and Global Change, Universidad Autónoma Madrid, Madrid, Spain, <sup>6</sup> Plant Molecular Biology Group, International Centre for Genetic Engineering and Biotechnology (ICGEB), New Delhi, India, <sup>7</sup> Department of European and Mediterranean Cultures: Architecture, Environment, and Cultural Heritage (DICEM), University of Basilicata, Potenza, Italy, <sup>8</sup> Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh, <sup>9</sup> Laboratory of Plant Stress Responses, Department of Applied Biological Science, Faculty of Agriculture, Kagawa University, Takamatsu, Japan

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Anna N. Stepanova,  
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United States

### \*Correspondence:

Naser A. Anjum  
dnaanjum@gmail.com  
Sarvajeet Singh Gill  
srgill14@yahoo.co.in

<sup>†</sup> These authors share first authorship

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## Editorial on the Research Topic

### Recent Insights Into the Double Role of Hydrogen Peroxide in Plants

Reactive oxygen species (ROS) of varied types can be yielded in plants at several primary sites (such as the chloroplast, mitochondria, and peroxisomes) under normal aerobic metabolism *via* processes including photosynthetic and respiratory electron transport chains. However, impaired oxidant-antioxidant balance and extreme growth conditions in plants are bound to cause increases in the cellular concentrations of radical and non-radical ROS such as superoxide anions (O<sup>2•-</sup>), hydroxyl radical (OH•), singlet oxygen (<sup>1</sup>O<sup>2</sup>), and hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>). On the one hand, H<sub>2</sub>O<sub>2</sub> has no unpaired electrons and is moderately reactive. Owing to its relative stability compared to other ROS and its capacity for diffusing through aquaporins in the membranes and over more considerable distances within the cell (Bienert et al., 2007), H<sub>2</sub>O<sub>2</sub> acts as a stress signal transducer and contributes to numerous physiological functions in plants. On the other hand, H<sub>2</sub>O<sub>2</sub> is a relatively long-lived molecule with a half-life of 1 ms, readily crosses biological membranes, and consequently can bring oxidative consequences far from the site of its formation (Neill et al., 2002; Sharma et al., 2012; Sehar et al., 2021). The Frontiers Research Topic “Recent Insights into the Double Role of Hydrogen Peroxide in Plants” highlighted the major mechanisms underlying the dual role of H<sub>2</sub>O<sub>2</sub> in response to different abiotic stresses in plants. This Research Topic incorporated 19 publications, including 10 original research articles, 8 reviews, and one perspective article.

## H<sub>2</sub>O<sub>2</sub>-METABOLISM AND H<sub>2</sub>O<sub>2</sub>-PRIMING ROLES IN ABIOTIC STRESS MANAGEMENT

As a potent signaling molecule H<sub>2</sub>O<sub>2</sub> gets produced in routine in stressed or non-stressed conditions *via* dismutation of O<sup>2•-</sup> radicals through superoxide dismutase (SOD) during electron transport in different compartments of the plant

cell, and is involved in the regulation of the plant growth, metabolism, and stress tolerance. It has also been noted that at higher concentrations in the cell during oxidative stress, ROS, including H<sub>2</sub>O<sub>2</sub>, can oxidize vital biomolecules (like nucleic acids, proteins, and lipids) and significantly impacts the seed germination process (Wojtyła et al.). Among the major abiotic stress factors, several heavy metals provoke increases in the production of ROS through plasma membrane-bound NADPH oxidases. However, the relationship of H<sub>2</sub>O<sub>2</sub> has also been established in heavy metal tolerance in crop plants (Cuypers et al.). H<sub>2</sub>O<sub>2</sub> directly mediates metal-induced oxidative signaling, where the production of H<sub>2</sub>O<sub>2</sub> may involve H<sub>2</sub>O<sub>2</sub> receptors, redox-sensitive transcription factors and inhibition of phosphatases (Miller et al., 2008). H<sub>2</sub>O<sub>2</sub> sensing in metal-exposed plants also involves activation of mitogen-activated protein kinase (MAPK) pathways (Opdenakker et al., 2012). Additionally, interaction of H<sub>2</sub>O<sub>2</sub> with Ca<sup>2+</sup> (Baliardini et al., 2015), NO (Arasimowicz-Jelonek et al., 2012) and oxylipins (Tamás et al., 2009; Keunen et al., 2013) was also reported in metal-exposed plants. Though excess accumulation of H<sub>2</sub>O<sub>2</sub> and polyamines (PAs) can be detrimental for the plant cell leading to premature cell death, a fine-tuning of these signaling molecules (H<sub>2</sub>O<sub>2</sub> and PAs) can result in stress management by coordinating intra-cellular and systemic signaling systems (Gupta et al.). Polyamine oxidase (PAO)-induced production of H<sub>2</sub>O<sub>2</sub> was found to be involved in the coleorhiza-limited rice seed germination (Chen et al.). ROS-specific probe DCFH2-DA enabled confocal laser scanning microscopy revealed a high level of ROS in the stigma at different developmental stages (unopened flower buds, recently opened flowers, dehiscent anthers, and flowers after fertilization) of scrutinized plants (Zafra et al.).

During evolution, plants have developed an efficient ROS-scavenging system constituting an array of enzymatic (SOD; CAT, catalase; APX, ascorbate peroxidase; GR, glutathione reductase; MDHAR, monodehydroascorbate reductase; DHAR, dehydroascorbate reductase; GPX, glutathione peroxidase; GOPX, guaiacol peroxidase, and GST, glutathione-S-transferase) and non-enzymatic (AsA, ascorbic acid; GSH, glutathione; phenolic compounds, alkaloids, non-protein amino acids, and  $\alpha$ -tocopherols) antioxidants to get rid of excessive ROS in the cell (Singh et al.). Notably, NADH oxidase (RBOH), alternative oxidase (AOX), the plastid terminal oxidase (PTOX), and the malate valve with the malate dehydrogenase isoforms are involved in maintenance of the cellular redox homeostasis under salinity stress (Hossain and Dietz). In *Arabidopsis* cell suspension cultures, anoxia stress/shock led to significant increases in H<sub>2</sub>O<sub>2</sub> (and also nitric oxide, NO); however, re-oxygenation maintained the components of ROS scavenging machinery like ascorbate-glutathione (AsA-GSH) system,  $\alpha$ -tocopherol, and eventual cell survival as result of decreased H<sub>2</sub>O<sub>2</sub> (Paradiso et al.). *Eutrema salsugineum* (halophyte) and *Arabidopsis thaliana* (glycophyte) exhibited a differential pattern of accumulation and scavenging of ROS. In particular, compared to *A. thaliana* chloroplasts, *E. salsugineum* chloroplasts showed a constitutive increase and the cell's steady-state regulation of H<sub>2</sub>O<sub>2</sub> level which prepared this plant for ROS-control mainly due to an efficient ROS-scavenging machinery including glucosinolates content and

well-coordinated tuning of hormonal signaling (Pilarska et al.). Elevation in the cellular level of H<sub>2</sub>O<sub>2</sub> and its consequences can be controlled by brassinosteroids, a class of plant-specific essential steroid hormones. To this end, in tomato seedlings, brassinosteroid (24-epibrassinolide) ameliorated the impacts of zinc oxide nanoparticles-caused elevated H<sub>2</sub>O<sub>2</sub> by enhancing the activity of enzyme involved in superoxide-dismutation (SOD), H<sub>2</sub>O<sub>2</sub>-metabolizing enzymes (catalase, CAT; and APX), increasing GSH-regeneration (as a result of increased GSH reductase activity; and consequently decreasing GSH-oxidation), finally inducing the transcripts of *Cu/Zn SOD*, *GSH1*, *CAT1*, and *GRI* (Li et al.). In a comprehensive *in silico* study, APX and GSH-peroxidase (GPX) genes/proteins from 18 different plant species were identified and compared in order to unravel their significance in excessive H<sub>2</sub>O<sub>2</sub> management (Ozyigit et al.). Notably, APX and GPX were found to be involved in the metabolism of antioxidants and secondary metabolites, redox homeostasis, stress adaptation, and photosynthesis/respiration. The major redox proteins namely plant peroxiredoxins (Prxs) and sulfiredoxins (Srxs) are involved in antioxidant defense and redox signaling in stressed plants. Srxs were also found to be involved in antioxidant defense and redox signaling in response to environmental stimuli; post-translational modifications of Srxs regulate the ROS-transduction and bioactivity. On the other hand, Prxs are sensitive to glutathionylation. Investigation of the glutathionylation of recombinant chloroplastic 2-Cys Prx and mitochondrial Prx IIF of pea plants revealed glutathionylation-mediated change of the decameric form of 2-Cys Prx into its dimeric glutathionylated form. Additionally, the reduced dimeric form of Prx IIF was glutathionylated without changing its oligomeric state (Calderón et al.). Thus, glutathionylation was argued to depend on the GSH/GSSG ratio owing to the perceptible difference in the exact effect on the 2-Cys Prx and Prx IIF proteins.

H<sub>2</sub>O<sub>2</sub>-priming (exposure of seeds, seedlings, or plants to stressors/chemical compounds that makes them ready to tolerate the later stress events) helps in biotic and abiotic stress tolerance in various crop plants by triggering the ROS scavenging machinery (Dikilitas et al., 2020). Exogenous supply of H<sub>2</sub>O<sub>2</sub> can induce stress tolerance under salt, drought, chilling, high temperatures, and heavy metal stress (Hossain et al.). In a study on mustard (*Brassica juncea* L.) cultivars, H<sub>2</sub>O<sub>2</sub>-induced reversal of the major negative impacts of Ni stress (200 mg Ni kg<sup>-1</sup> soil) led to increased photosynthetic nitrogen-use efficiency, sulfur-use efficiency, and GSH content and decreased levels of lipid peroxidation and electrolyte leakage (Khan et al.). Notably, H<sub>2</sub>O<sub>2</sub> priming-mediated increased tolerance to cadmium-caused oxidative stress in *Brassica napus* involved fine-tuning between the glyoxalase system and the components of ROS-scavenging machinery (Hasanuzzaman et al.).

## H<sub>2</sub>O<sub>2</sub> CROSSTALK WITH OTHER MOLECULES

Along with H<sub>2</sub>O<sub>2</sub>, other signaling molecules (such as nitric oxide, NO; and calcium, Ca<sup>2+</sup>) and phytohormones (such as jasmonic

acid, JA; salicylic acid, SA; and abscisic acid, ABA) play key roles in stress signaling cascades and crosstalk during plants' stress responses (Saxena et al., 2016). To this end, the crosstalk of H<sub>2</sub>O<sub>2</sub> with NO and Ca<sup>2+</sup> was argued to contribute to regulation of the plant development and abiotic stress responses (Niu and Liao). Notably, the role of SA in adventitious root formation involved H<sub>2</sub>O<sub>2</sub> acting as a downstream messenger (Yang et al., 2013). Having emerged as a master regulator of stress responses, ABA signaling pathway triggers significant changes in gene expression and plants' adaptive physiological responses (Saxena et al., 2016). There occurs a close relation among the MAPK cascades, ABA, JA, SA, and H<sub>2</sub>O<sub>2</sub> where exogenous application of H<sub>2</sub>O<sub>2</sub> triggers MAPK cascade, which in turn involves ABA, JA, and SA (Saxena et al.). ABA-induced H<sub>2</sub>O<sub>2</sub> accumulation can protect plant parts (such as pumpkin-grafted cucumber leaves) against Ca(NO<sub>3</sub>)<sub>2</sub> via ABA/H<sub>2</sub>O<sub>2</sub> signaling-led induction of ROS-scavenging machinery (Shu et al.). S-nitrosogluthione reductase (GSNOR) determines the level of S-nitrosothiol and thereby regulates NO-signaling in plants (Lindermayr, 2018; Jahnová et al., 2019). In *A. thaliana*, H<sub>2</sub>O<sub>2</sub> *in vitro* led to inhibition of the activity of GSNOR and significantly changed NO-homeostasis, which in turn resulted in the activation of ROS-scavenging machinery in order to suppress the oxidative damage (Kovacs et al.).

## CONCLUSIONS AND FUTURE PERSPECTIVE

In the current Research Topic “Recent insights into the double role of hydrogen peroxide in plants,” the contributions discussed

the versatile role of H<sub>2</sub>O<sub>2</sub> as a signaling molecule that triggers the upregulation of the components of antioxidant defense machinery and imparts tolerance in crop plants against the variety of environmental cues. The crosstalk of H<sub>2</sub>O<sub>2</sub> with other signaling molecules and phytohormones leads to signal transduction in response to various stresses and regulates plant growth, development, and stress tolerance. Therefore, further understanding on the coordination of H<sub>2</sub>O<sub>2</sub> and other signaling molecules NO, Ca<sup>2+</sup>, MAPK, SA, and ABA can pave the way to achieving tolerance in crop plants to increasing stress conditions.

## AUTHOR CONTRIBUTIONS

NA and SG prepared the first draft of the manuscript. FC, CO-V, LH, NT, AS, MH, and MF read and revised the manuscript. All authors listed approved the final version for publication.

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